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MORPHOLOGY OF THE LEGS OF HYMENOPTEROUS INSECTS.[1]

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ACCORDING to our modern philosophy regarding the origin and development of animal organs and organisms, we should look at such organs as are much used in the animal economy to find extremes in modification. Thus among mammals the teeth are

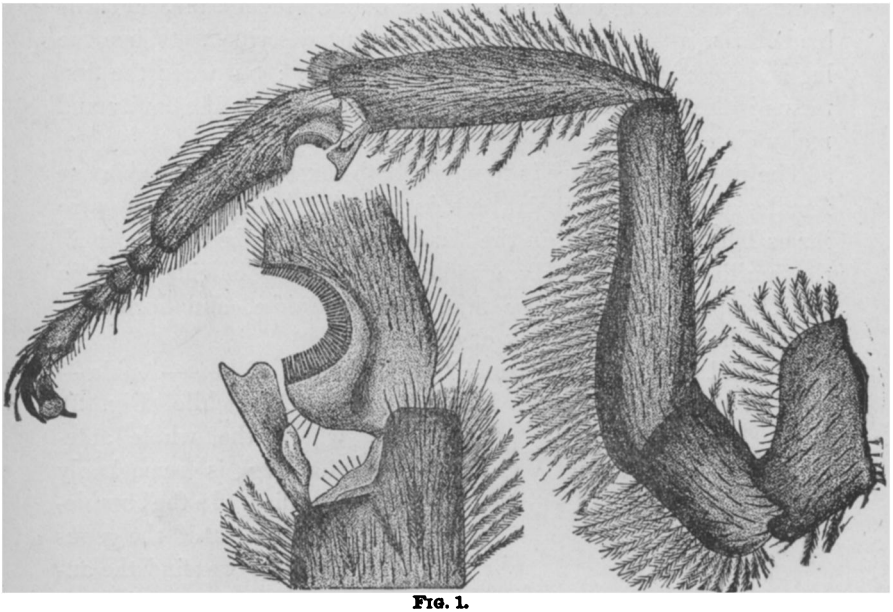

FIG. 1.

[1] This paper was read before American Association for Advancement of Science, in August, 1887, at N. Y. meeting.

most modified and very important in systematic mammalogy. For like reason the ornithologist looks to bill and feet in his study of families and genera. With the laws of variation and adaptation before us, we should expect to find modification carried to extremes among Hymenopterous insects. The life functions of these insects are so wonderful and varied that a maximum differentation of organs and structure is required for their execution. The chief tools used by these Hymenopterons are the legs and mouth organs, and it is to the former that I invite attention.

Let us consider the anterior or prothoracic legs of the honey-bee. We first notice (Fig. 1) a strong and interesting modification in the basal tarsus and tibial spur, which modification is known as the "antenna cleaner." At the base of the first tarsal joint and in the angle between it and the tibia is a short, hollow semi-cylinder. The concave surface of this cavity is smooth except at the outside margin, where there are from seventy-eight to ninety projecting hairs, which under the microscope remind one of the villi of the small intestines of mammals. These teeth, like hairs, projecting as a fringe, form a most delicate brush. The tibial spur is so modified as to resemble a very short handled razor, the blade of which is for a wide space facing the tarsus, a most delicate membrane, and this blade forms a sort of lid to the cavity just described. When the leg is straight this lid barely reaches the cavity; but when the first tarsus is flexed upon the tibia it serves as a cover to the cavity and really closes it.

The peculiar structure is found in both sexes and in the abortive females or workers of social bees, in all other bees, in all wasps so far as I have examined, in the Mutillidæ, Formicidæ in ants, in all the families of parasitic Hymenoptera except the Chalcids, while in the Cynips, Cynipidæ, Saw flies, Tenthredinidæ, and horn-tails, Uroceridæ, we find it nearly or quite absent.

We find the "antenna cleaner" in all species of bees—Apidæ—even in the curious species like the male of Megachile (Fig. 2), where the whole anterior leg is remarkably modified. In the bumble-bees species of the genus Bombus we find the antenna cleaner almost

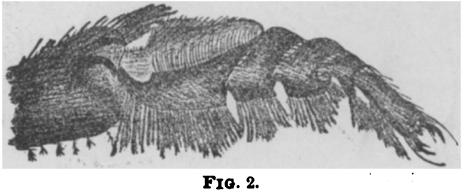

FIG. 2.

exactly like that of the honey-bee, except the part which I have termed the blade, in the modified tibial spur has its back more extended, and the whole back of the blade and the extended point thickly set with short spines, reminding one of the serrations on the antennæ of many beetles like the Buprestids. In the carpenter-bees—Xylocopa—there is no variation from the type of the Bombus except the serrated margin of the blade is still more marked. In the female of the tailor-bees—Megachile—the extended point and serrations are both absent, and we have again the form of this organ in the honey-bee. The number of the teeth in the cavity however, is less, there being from forty-five to fifty. In Osmia and Andrena (Fig. 3), the arrangement is much as in the Xylocopa; in Nomada the serrations are less spinous and more scattered, while in the beautiful species of Angochlora the cavity is quite shallow, the blade of the spur narrow, and the spines on the back and point of the blade slim and hair like.

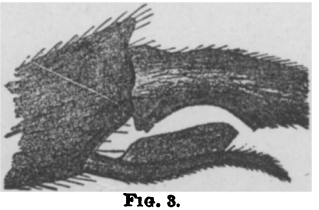

Fig. 3.

In the several families of wasps we find this pollen cleaner, well developed, and in some cases quite modified from the same in bees. In the paper-making wasps—Vespidæ—it is much as in the lowest bees—Nomada and Angochlora. The cavity is more shallow than in the honey-bee, the membranous portion of the blade is quite narrow, and the appendages on the point of the blade are hair-like, though those near the base remind one of saw teeth.

In sand-wasps—Bembecidæ—this organ is much as seen in bees and paper-making wasps; though the point of the blade is very long, and the back and point both thickly set with fine hairs.

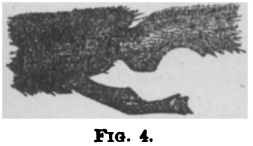

Fig. 4.

In all species of mud wasps, belonging to the family Sphegidæ (Fig 4) we find an interesting modification in the spur. Here the membranous portion of the blade is nearly obsolete, while its inner margin is concave and fringed with a toothed brush much as seen in the cavity, though the teeth are shorter. The end of the blade is blunt, and bears from five to eight heavy appendages, which, when magnified, look like so many fingers.

In the beautiful mud wasps of the family Pompilidæ, this apparatus is much as in the Sphegidæ, except that the cavity is more shallow. The fringe on the spur is peculiarly fine and beautiful. The spur is pointed, the point being flat and margined on both sides with spines.

In the Mutillidæ this organ is specially well shown. The type is that of the bees and Vespidæ, as the blade is membranous and without the fringe. The back and both sides of the point, however, are covered with a row of spinous hairs.

In the ants—Formicidæ—(Fig 5) the cavity is shallow and the fringe well marked in the cavity and on the spur where it is double, and while this brush is beautiful, it is not widely different from the hairs on the point of the blade, and on the remaining part of the basal tarsus.

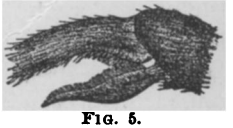

Fig. 5.

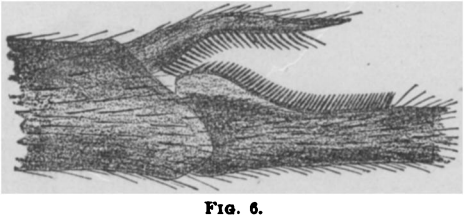

Fig. 6.

In Ichneumonidæ (Fig. 6), and Braconidæ we find this antenna cleaner, less developed, though still present. The cavity is hardly more than an inclined plane, the rise at the distal end being very slight. The spur is marked by a distinct concavity, and the fringe is present in the cavity and on the spur, though the brush in case is made up of coarser hairs than are found in bees or wasps.

In the species of Chrysidæ we find this apparatus more perfect than in the Ichneumonidæ. The cavity is deeper, the spur concave, and both show the comb or fringe well marked. The species of this family are unique in that the concave spur is fringed to the very point of the blade.

In the minute Proctotrupidæ the antenna cleaner is even less developed than in the Ichneumon flies. The cavity is almost wholly obsolete, the spur is only slightly concave, and the hairs forming the brush are hardly different from the other hairs of the leg. In the Chalcid flies—Chalcididæ—the cavity is wholly absent, and the only suggestion of this apparatus is in the slightly curved spur. The brush is also obsolete. The same is hardly less true of the gall-

flies—Cynipidæ. In the saw-flies—Tenthredinidæ—(Fig. 7), there is no hint of the cavity on the first tarsus; but a slight concavity of the spur, with the membrane just visible, still suggests the "pollen cleaner." In the horn-tails—Uroceridæ—the only reminder we have of the antenna cleaner is in the slightly curved spur. The membranous part of the blade is wholly wanting.

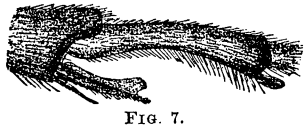

FIG. 7.

In the study of this apparatus I have been very much interested to note how persistent is its type within each family. I have carefully examined very numerous specimens, and I think we could, from the study of this organ alone, arrange the species of Hymenoptera, with very few exceptions, in their respective families. The same is also true in many cases of genera. We shall not wonder at this as we come to study the function of the organ and note its great importance.

No one who has studied bees closely can doubt for a moment the functional importance of the antennæ. As touch organs, they are most delicate and wonderful. The work of the hive bee is largely performed in total darkness. Yet very intricate operations are carried on with unerring exactness. This is only possible through the aid of those very sensitive tactile organs—the antennæ. There is hardly less doubt that the antennæ are the scent organs of insects. And with Hymenopterous insects, especially of the higher families, the sense of smell is of exceeding importance. It has been thought also that the antennæ serve as organs of hearing. This, however, is probably not true. We see then that it is of the highest importance that these organs be kept free from all dust. But the very habits of most Hymenopterous insects, visiting, as they do, flowers laden with pollen, as do all except the lowest families, or digging in the mud and dust, as do many bees and wasps, tend to soil the antennæ. And it is no more necessary for the microscopist to brush the lenses of his objectives than for the bee or wasp to dust its antennæ.

That the function of the apparatus just described is to brush or free from dust the antennæ is easily proved by experiment. We have only to imprison a bee or wasp on the window pane of our room, and quietly dust its antennæ with lime or flour, when we will see it pass an anterior leg forward, draw an antennæ through the

cleaner, after which the bee will pass the fore legs, now foul with dust, between the brushes formed by the soft hairy inner faces of the basal tarsi of the middle legs. This will be repeated several times, when upon examination the antennæ will be found entirely freed from the troublesome dust. In case of the wasp, as *Polistus annularis*, the antennæ are cleaned the same as just described except that the leg or antenn cleaner is cleanedæ by passing it between the jaws instead of between the middle legs. As we are sure of the function of this beautiful apparatus we do not need to refer to the wonderful correspondence in size of the cavity in each separate case, with the antennæ of the same insect, which would be added proof if such were needed as to its function. I will also state that I believe I have found an antennæ cleaner in some beetles, especially carabids. In these cases the cavity and lid are both on the tibia a little distance towards the body from its farther end.

In the honey-bee on the outer end of the tibia, just opposite the antennæ cleaner (Fig. 1), is a small brush. This has been regarded by some as a cleaner of the antennæ cleaners; but we have seen that the latter organs are cleaned in another way. I have never seen these brushes used to clean the cavities, though I have observed closely. The fact that other bees, wasps, ants, etc., have no such brush makes me doubt such function.

The branching, fluffy hairs which cover the upper part of the fore leg (Fig. 1) of the worker honey-bee are like the same in other legs of the same insect, of use in gathering the pollen. From these hairs the pollen is combed off and transported to the pollen baskets.

Opposite the side of the basal tarsus which contains the cavity of the antennæ cleaner of the bee (Fig. 1), is a comb formed of quite stiff hairs. This is used to free the hairy compound eyes of the bees of dust, pollen, etc., and also to comb the pollen off the lighter hairs. The former function may be observed by closer observation, as the bee is seen to wipe its pollen-begrimmed eyes, much as the common house fly is observed to rub its eyes, face and antennæ.

The middle legs of bees are covered with the compound hairs to the end of the tibia where a prominent tibial spur (Fig. 8) is seen, but no more prominent in the honey-bee than in other bees and in wasps. Indeed it is even larger in drones than in the

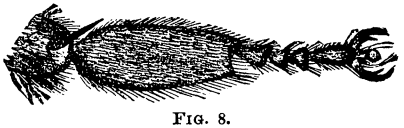

FIG. 8.

worker bees. It has been claimed that this is the lever with which the bee pries off the pollen mass into the cell; but the fact that these are no more prominent than in other insects where there is no such function to be performed, and the fact that the stiff hairs which point outward at the ends of these and all the legs are better fitted for this work, gives reason to question the accuracy of this view. On the inside of the first tarsal joint of the middle legs (Fig. 8) is a fine brush thickly set with hairs, which, as we have already seen, is used to clean the antennæ cleaner, and, as I often noticed large masses of pollen adhering to this brush, I am led to the conclusion that these are hands or claspers that aid to bear the pollen to the baskets on the posterior legs. The lower or outer hairs of this brush are spine-like and doubtless aid as already suggested in pushing the loads of pollen from the legs into the cells of the comb.

FIG. 9.

Upon the first three joints of the posterior legs, the coxa, trochanter and femur (Fig. 10) the soft, compound, polen gathering hairs are well shown. In the honey bee the tibia and first tarsus ars wonderfully developed. On the outside (Fig. 9) are cavities for holding the pollen. These shallow cavities, one in each of the joints, are bordered with course hairs, which serve as so many stakes to aid in holding the large pollen masses which the bee is often seen carrying to the hive. Opposite the concavity of the tarsal joint (Fig. 10) on the inside are to be seen nine or ten rows of beautiful yellow hairs, which form as many combs or brushes, which serve to collect and transport the pollen from different parts of the bee to the pollen baskets. If a bee is captured while collecting pollen,

these beautiful brushes will always be found with more or less pollen adhering to them. Of course the combs of one leg are used to fill the pollen basket of the opposite legs. As before stated, this work is in part performed by a similar but less perfect arrangement on the corresponding portion of the middle legs.

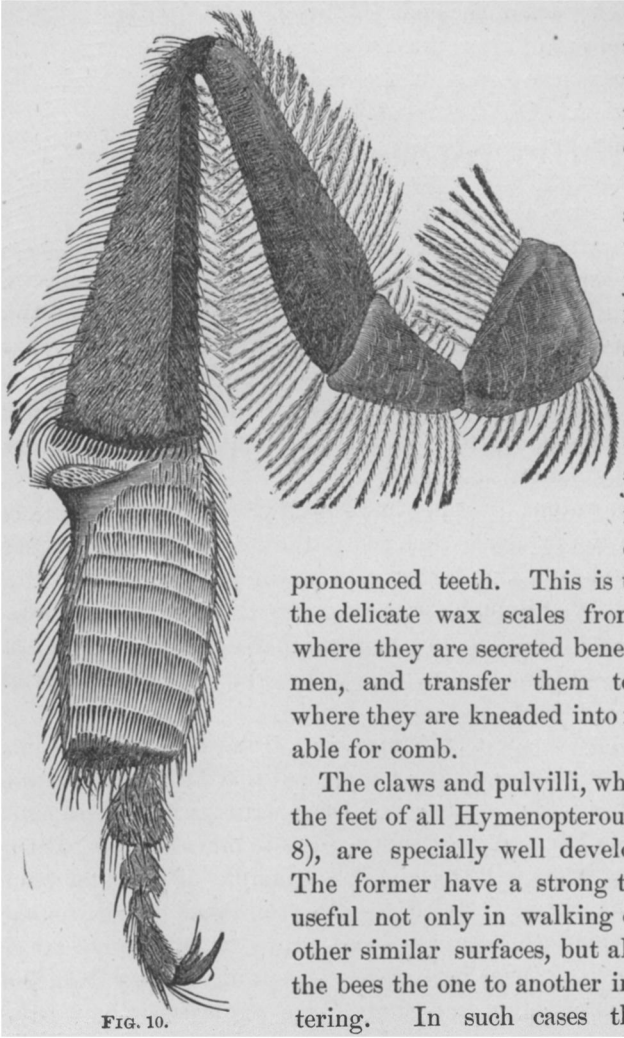

FIG. 10.

Between the tibia and first tarsus of the posterior legs of the honey-bee (Figs. 9 and 10) is a very curious joint, reminding one of a steel trap or the jaws of an animal, the tibial or inner jaw of which is well covered with quite pronounced teeth. This is used to grasp the delicate wax scales from the pockets where they are secreted beneath the abdomen, and transfer them to the mouth where they are kneaded into material suitable for comb.

The claws and pulvilli, which terminate the feet of all Hymenopterous insects (Fig. 8), are specially well developed in bees. The former have a strong tooth and are useful not only in walking on wood and other similar surfaces, but also in holding the bees the one to another in case of clustering. In such cases the uppermost have to sustain hundreds of their fellows, and this often for hours. There are few better examples in the whole animal kingdom of what may be accomplished by mere muscle.

The pulvilli are situated between the claws. They are large and glandular, and by secreting a viscid adhesive material enable a bee to walk up a smooth surface like that of glass. We thus understand why a bee fails in its attempt to walk up a moistened or powdered glass surface. When a bee walks on wood the pulvilli are turned back, when on glass the claws are similarly made to change their position.

DIRECTIVE COLORATION IN ANIMALS.

BY J. E. TODD.

MUCH has been written by Wallace, Darwin and others concerning the protective effects of coloration in animals, and this adaptation perhaps accounts for most of the chromatic characteristics of animals. Darwin has also shown how many may be accounted for by sexual selection, and Wallace has referred many of those, still remaining unexplained, to the play of color-producing forces uncontrolled by natural selection.

So far as the author is aware, however, there has been no distinct enunciation of the principle sketched in the following pages. The nearest approach to it is a remark of Darwin in regard to the rabbit's white tail—that it might serve as guide to the young in following the old ones to the burrow; and another—that the stripes of the zebra may be of use to stragglers in recognizing their fellows at a distance. (Vide AM. NAT., 1877.)

Wallace approves the suggestion, and, from some notes of his recent Baltimore lectures, it may be inferred that he has carried the principle further. But in their published writings both these eminent naturalists refer several distinct cases to other sources, which in the following pages will be claimed as examples of what, for want of a better name, we have styled *directive coloration.* And whether the views hereinafter to be advanced prove to be entirely novel or not, they have, so far as here expressed, sprung entirely from the author's own observation and study. He regrets that both have necessarily been so limited that he cannot multiply examples as freely as nature has supplied them. What is here offered is only a sketch of what might be wrought out by any one having time to carry out the work in its details.